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Abundance and phenology of Pseudoscorpiones (Arachnida) from a mixedwater inundation forest in Central Amazonia, Brazil

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Abundance and phenology of Pseudoscorpiones (Arachnida) from a mixedwater inundation forest in Central Amazonia, Brazil. - A total of 675 Pseudoscorpiones, representing nine species, were captured during 12 months in an inundation forest near Manaus, which is covered by several meters of mixedwater for 5-7 months each year. In the terrestrial phase, the average abundance of pseudoscorpions in the soil (0-14 depth) was three times higher during the rainy season (140 ind./m^2/month) when compared to the season with less rainfall (48 ind./m^2/month). A survival strategy in response to flooding was observed in the terricolous and univoltine *Tyrannochthonius amazonicus* (Chthoniidae): immature tritonymphs, representing a migrating stage, moved from the soil to the trunk/canopy region where they passed the aquatic phase. *Pseudochthonius homodentatus* (Chthoniidae) changed from a terricolous mode of life in Central Amazonian upland forests to an arboricolous living in the inundation forest. Six other species, obtained in low numbers predominantly in the trunk/canopy region, are considered arboricolous as well. Our data reconfirm that seasonally inundated forests of the mixedwater type near Manaus represent an ecotone: *Pachychernes baileyi* (Chernetidae), *Tyrannochthonius amazonicus* (Chthoniidae), *Geogarypus amazonicus* (Geogarypidae), *Pachyolpium irmgardae* (Olpiidae) and *Dolichowithius minutus* (Withiidae) inhabit blackwater inundation forests in the valley of the Negro River. *Parachernes adisi* (Chernetidae) was collected from whitewater inundation forests along the lower Solimões River. *Paratemnoides minor* (Atemnidae) occurs in black- and whitewater inundation forests. *Pseudochthonius homodentatus* (Chthoniidae) lives in primary and secondary (non-flooded) upland forests of Central Amazonia. The occasionally phoretic *Lechytia chthoniiformis* (Chthoniidae) is found throughout South America.

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INTRODUCTION

Forests in the Central Amazon region are divided into non-flooded upland forests and inundation forests (BRAGA 1979). The period of flooding (= aquatic phase) in seasonal inundation forests (PRANCE 1979) varies from 5 to 7 months a year and is caused by a monomodal flood pulse (JUNK *et al.* 1989). Terrestrial invertebrates that inhabit these forests stay in the area and make use of various survival strategies or, when possible, migrate to adjacent upland (= terra firme) forests before the beginning aquatic phase (ADIS 1997). In this study we present the reaction of Pseudoscorpiones to flooding as well as the abundance and phenology of the species found in a seasonal mixedwater inundation forest near the city of Manaus in the northern region of Brazil.

STUDY AREA, MATERIAL AND METHODS

The experimental area was at Lago Janauarí (03°20'S, 60°17'W), located on a strip of land between the Negro and Solimões Rivers, about 10 km distant from Manaus. The region was influenced by blackwater of the Negro River during low water-level and by whitewater of the Solimões River during the high water period. Terrestrial arthropods were collected from July 1987 to June 1988. The study area was inundated until the end of July 1987 and from June 1988 onwards (terrestrial phase: August 1987 - May 1988). The Pseudoscorpiones were monitored in the soil and at the soil surface (terrestrial phase) as well as on the lower part of tree trunks (terrestrial and aquatic phases):

During the terrestrial phase, six soil samples were taken monthly, along a transect. Their combined area represented 0.21m^2. Each sample, 14 cm in depth, was subdivided into four subsamples of 3.5 cm each. Pseudoscorpiones were extracted from subsamples following a modified method of Kempson (ADIS 1987). Four ground photo-eclectors (= emergence traps) and seven pitfall traps (= Barber traps) were placed on the forest floor to collect pseudoscorpions from the soil surface. The vertical migration of Pseudoscorpiones on tree trunks was detected by weekly samples with arboreal photo-eclectors (= trunk traps) directed upwards and downwards on one tree trunk each. Further information on sampling techniques and the study site are given in ADIS (1981), ADIS *et al.* (1996) and FUNKE (1977).

In addition, the presence of Pseudoscorpiones was checked in soil samples which were taken under water at the end of the aquatic phase (late August 1988) as described above and subsequently extracted by means of a flotation method via sugar water (for methodology see ADIS *et al.* 1989). The presence of Pseudoscorpiones in tree crowns was tested by fogging canopies with natural pyrethrum during the aquatic phase (early August 1979; cf. ERWIN 1983).

Collection data were statistically evaluated by means of linear correlation (CAVALLI-SFORZA 1972) with local abiotic factors (temperature, pH and humidity of the soil, as well as temperature and relative humidity of the air and precipitation).

Seasonal inundation forests in Central Amazonia are subject to a rainy season (December-May: average precipitation 1550 mm), and a "dry" season (June-November: average precipitation 550 mm, but each month has some rain events; cf. RIBEIRO & ADIS 1984).

The taxonomic work for this paper was done by V. Mahnert (cf. MAHNERT 1979; MAHNERT & ADIS 1985), the collection and evaluation of field data by J. Adis, J.W. de Morais and E. Berti-Filho. Pseudoscorpiones sampled were classified as protonymphs, deutonymphs, tritonymphs, adult males and females.

RESULTS AND DISCUSSION

A total of 675 Pseudoscorpiones, representing nine species, were sampled from the experimental area. Out of these, 34.2% were obtained in the soil, 28.5% from the soil surface (26.4% in emergence traps, 2.1% in pitfall traps) and 37.3% from trees (14.4% in upwards directed, 21.3% in downwards directed trunk traps and 1.6% in the canopy).

Only 1.4% of the total Arthropoda extracted from the soil (Acari and Collembola omitted; cf. MORAIS 1995) were Pseudoscorpiones (n=231). Of these, 95.2% were represented by *Tyrannochthonius amazonicus* (Chtoniidae), 2.6% by *Pachyolpium irmgardae* (Olpiidae) and 2.2% by *Pseudochthonius homodentatus* (Chthoniidae). These species were most frequent within the first 3.5 cm of soil depth (Fig. 1). Their greatest abundance occurred in February 1988 (rainy season), with 24.2% of the total catch being extracted from the soil (270 ind./m^2; Fig. 2). Averages of 48 ± 68 ind./m^2/month were collected in the dry season and 140 ± 113 ind./ m^2/month in the rainy season. Of the total Pseudoscorpiones extracted from the soil, 20% (22 ± 20 ind./m^2/month on average) were represented by protonymphs, 22% (25 ± 28 ind./m^2/month on average) by deutonymphs, 30% (33 ± 30 ind./m^2/month on average) by tritonymphs, 15% (16 ± 15 ind./m^2/month on average) by males and 13% (14 ± 13 ind./m^2/month on average) by females. No Pseudoscorpiones were found in soil materials taken underwater during the aquatic phase. Five specimens were obtained by fogging the canopy during the aquatic phase.

The highest abundance of pseudoscorpions recorded in the soil of the mixed-water forest (265 ind./m^2 in February 1988) was lower than that found in a forest flooded by blackwater in the valley of the Negro River (655 ind./m^2 in January 1981; ADIS & MAHNERT 1985).

Tyrannochthonius amazonicus (Chthoniidae)

This was the most abundant species in the experimental area (cf. Fig. 1). Its highest "activity density" (SCHAEFER 1992) was observed during the rainy season of the terrestrial phase. Reproduction started at the end of the dry season and lasted throughout the rainy season (Fig. 2). The first protonymphs were collected in October 1987 by soil extration. During the following months, deutonymphs and tritonymphs

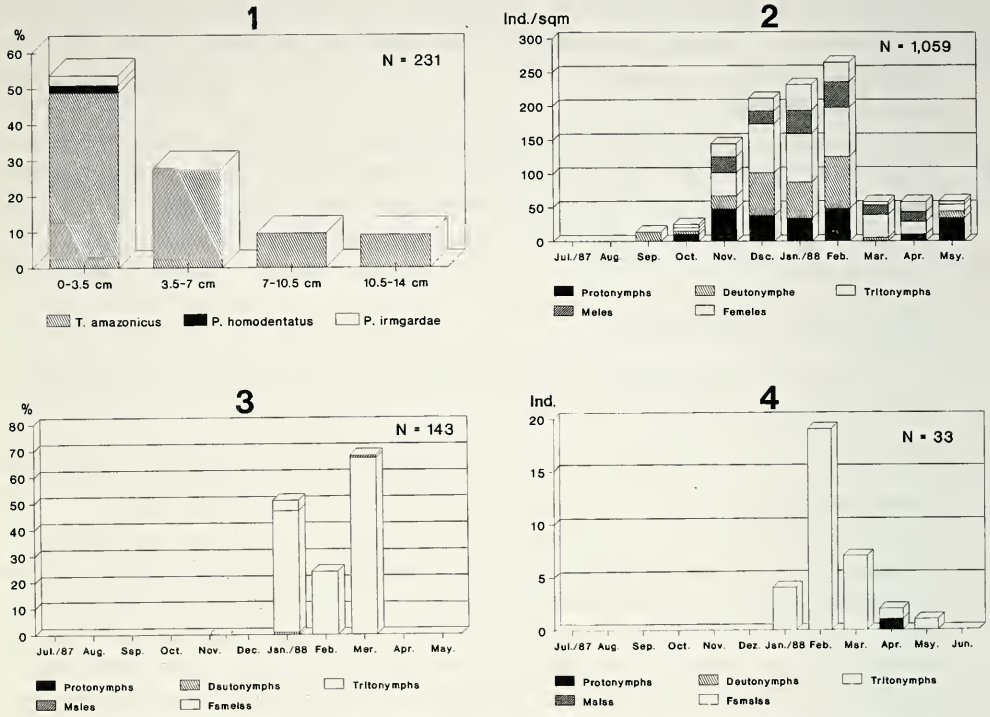

FIG. 1. Vertical distribution of pseudoscorpion species in the soil. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and May, 1988 (terrestrial phase) in a seasonal mixedwater inundation forest of Central Amazonia. Total catch (N) = 100%.

FIG. 2. *Tyrannochthonius amazonicus* (Chthoniidae): Temporal occurrence and abundance of developmental stages (ind./m^2) in the soil. Monthly samples (0-14 cm soil depth) taken between August, 1987 and May, 1988 (terrestrial phase) in a seasonal mixedwater inundation forest of Central Amazonia.

FIG. 3. *Tyrannochthonius amazonicus* (Chthoniidae): Temporal occurrence of developmental stages captured in ground photo-eclectors between August, 1987 and May, 1988 (terrestrial phase) in a seasonal mixedwater inundation forest of Central Amazonia. Total catch (N) = 100%.

FIG. 4. *Tyrannochthonius amazonicus* (Chthoniidae): Temporal occurrence of developmental stages captured in one arboreal photo-eclector for trunk ascents between July, 1987 and June, 1988 in a seasonal mixedwater inundation forest of Central Amazonia.

increased in number (Fig. 2). Males and females were occasionally captured on the forest floor with pitfall traps. Our extraction data also suggested that the lifetime of the adults was restricted to the terrestrial phase (Fig. 2). Tritonymphs came to the soil surface (Fig. 3), moved to the trunk/canopy region (Fig. 4) where they passed flooding, and returned to the forest floor at the end of the aquatic phase (Fig. 5). Upward migration occurred mainly in February/March 1987 (Fig. 4), during the rainy season. The number of tritonymphs captured during trunk ascents was higher than that obtained during trunk descents (Figs 4, 5). ADIS (1981) suggested, that many tritonymphs suffer

predation during their forced stay in the trunk/canopy region. In addition, some tritonymphs have moulted during their downward migrations because the first adults were captured on tree trunks at the end of the aquatic phase (Fig. 5). They were smaller in size when compared to adults from the forest floor. The low number of proto- and deutonymphs on the forest floor and in the trunk/canopy region confirm data by ADIS & MAHNERT (1985) which indicated that these instars live mostly in the soil.

With respect to the vertical distribution in the soil, tritonymphs were most abundant in the upper soil layer (Fig. 6), whereas protonymphs were more abundant in the mineral subsoil below the organic layer (3.5-7 cm soil depth). One possible explanation to this fact is, that they are less active and thus more susceptible to predation, which is more intense near the soil surface (cf. MORAIS 1995; ADIS 1997). Results from the correlations between the vertical distribution of *T. amazonicus* and the local abiotic parameters showed that the population density decreased from the upper to the lower soil layers with increasing soil humidity ($p<0.01$, $r=-0.9905$; $n=4$ in March and $p<0,001$, $r=-0.9999$; $n=4$ in April 1988), with decreasing soil temperature ($p<0.01$, $r=+0.9980$, $n=4$ in February and $p<0.05$, $r=+0.9802$, $n=4$ in March 1988), and with decreasing pH of the soil ($p<0.01$; $r=+0.9901$ $n=4$ in March and $p<0.05$, $r=+0.9897$, $n=4$ in April 1988). Changes in abiotic parameters on the experimental area occurred with the beginning rainy season (cf. data in MORAIS 1995).

The results of *T. amazonicus* from the mixedwater inundation forest coincide with those obtained by ADIS & MAHNERT (1985) from a blackwater inundation forest in the valley of the Negro River. The nocturnal tritonymphs represent migratory stages which pass inundation of 5-7 months duration mostly under loose bark in the trunk/canopy region and return to the forest floor at the end of the aquatic phase. However, upward migration of trionymphs in the blackwater inundation forest was recorded mostly 2-3 weeks before the beginning aquatic phase (in March) whereas in the mixedwater inundation forest tritonymphs ascended tree trunks 14 weeks before the forest floor was flooded (in February; Fig. 4).

According to the ecological classification of terrestrial invertebrates from Central Amazonian inundation forests (cf. ADIS 1997), *T. amazonicus* represents a terricolous migrating species. It is considered endemic to black- and mixedwater inundation forests as it is neither found in non-flooded upland forests of Central Amazonia nor in whitewater inundation forests along the lower Solimões River (cf. ADIS 1981, MAHNERT & ADIS 1985).

Pseudochthonius homodentatus (Chthoniidae)

In the soil, this species represented only 2.2% (0.5 ± 1.1 ind.m^2/month on average) of the total pseudoscorpions. Animals were exclusively obtained from the organic layer (0-3.5 cm), 80% represented adults and 20% tritonymphs.

On the soil surface, *P. homodentatus* was only captured during the rainy season of the terrestrial phase (12/87-3/88). Abundance in emergence traps was 11 ± 21 ind./m^2/month on average, 68% of all specimens were adults and 32% deuto- and tritonymphs.

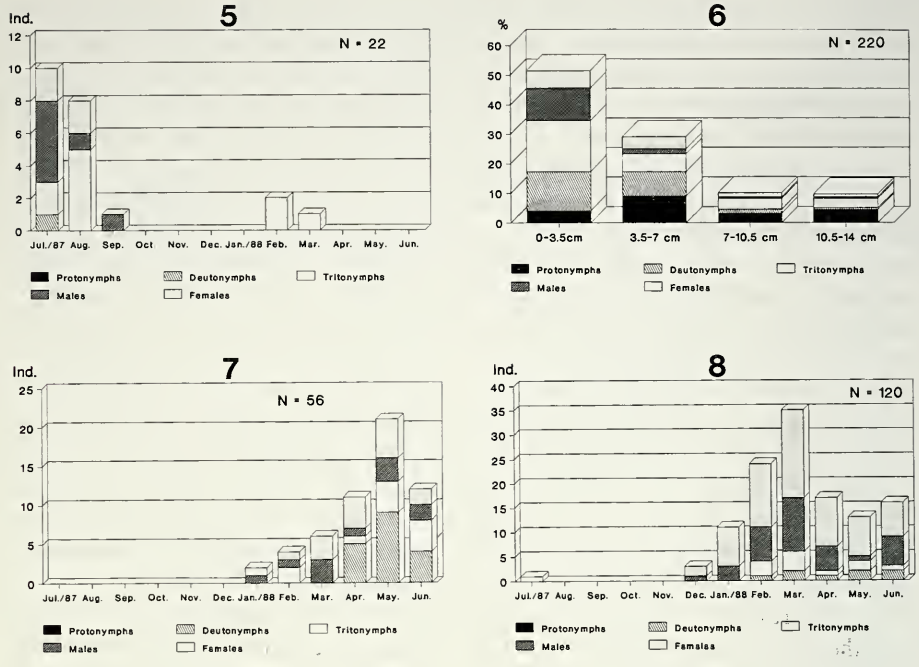

FIG. 5. *Tyrannochthonius amazonicus* (Chthoniidae): Temporal occurrence of developmental stages captured in one arboreal photo-eclector for trunk descents between July, 1987 and June, 1988 in a seasonal mixedwater inundation forest of Central Amazonia.

FIG. 6. *Tyrannochthonius amazonicus* (Chthoniidae): Vertical distribution of developmental stages in the soil. Monthly samples taken every 3.5 cm to a depth of 14 cm between August, 1987 and May, 1988 (terrestrial phase) in a seasonal mixedwater inundation forest of Central Amazonia. Total catch (N) = 100%.

FIG. 7. *Pseudochthonius homodentatus* (Chthoniidae): Temporal occurrence of developmental stages captured in one arboreal photo-eclector for trunk ascents between July, 1987 and June, 1988 in a seasonal mixedwater inundation forest of Central Amazonia.

FIG. 8. *Pseudochthonius homodentatus* (Chthoniidae): Temporal occurrence of developmental stages captured in one arboreal photo-eclector for trunk descents between July, 1987 and June, 1988 in a seasonal mixedwater inundation forest of Central Amazonia.

On tree trunks, *P. homodentatus* was captured during the rainy season and the beginning dry season (n=176; Figs 7, 8). Most animals were obtained in arboreal photo-eclectors for trunk descents (68%) when compared with the catches in traps for trunk ascents (32%). About 15% of all specimens represented deutonymphs, 13% tritonymphs and 72% adults (47% females, 25% males).

According to the classification of ADIS (1997), *P. homodentatus* represents an arboricolous migrating species which has its main reproduction in the trunk/canopy region and a secondary reproduction on the forst floor during the terrestrial phase.

However, in primary and secondary (non-flooded) upland forests *P. homodentatus* was only found on the forest floor (MAHNERT & ADIS 1985; ADIS & MAHNERT 1990, 1993). This suggests an adaptation towards an arboreal life in mixed- and blackwater inundation forests, similar to that reported for *Brazilatemnus browni* (Miratemnidae; ADIS *et al.* 1988).

OTHER PSEUDOSCORPION SPECIES

The following seven species were collected in low numbers:

All developmental stages of *Pachyolpium irmgardae* (Olpiidae) were obtained during the rainy season (12/87-5/88) from the organic soil layer (n=6), on the soil surface (emergence traps; n=13) and on tree trunks (n=5). Our data reinforce the view that this pseudoscorpion represents an arboricolous migrating species (cf. ADIS & MAHNERT 1985; MAHNERT & ADIS 1985) which is endemic to black- and mixedwater inundation forests.

Geogarypus amazonicus (Geogarypidae; 1♂, 1♀, 1 protonymph) was captured in trunk traps. *Paratemnoides minor* (Atemnidae; 5♀♀), *Parachernes adisi* (Chernetidae; 4♂♂), *Pachychernes baileyi* (Chernetidae; 1♂) and *Dolichowithius minutus* (Withiidae; 1♂) were obtained by fogging the canopy. All these pseudoscorpions are regarded as arboricolous non-migrating species (ADIS 1981; ADIS & MAHNERT 1985).

Lechytia chthoniiformis (Chthoniidae; 1♂) was captured on the forest floor with emergence traps. This pseudoscorpion species is found throughout South America (cf. HARVEY 1991). In Amazonia, it was reported to be phoretic on the cerambycid beetle *Stenodontes spinibarbis* (AGUIAR & BUERNHEIM 1991, 1992).

CONCLUSIONS

T. amazonicus is a terricolous, univoltine species and most abundant in the organic soil layer. The migration of tritonymphs from the soil to the trunk/canopy region is regarded as a survival strategy in response to the flood pulse.

P. homodentatus changed from a terricolous mode of life in Central Amazonian upland forests to an arboricolous living in mixed- and blackwater inundation forests.

Our results are in line with the hypothesis that seasonally inundated forests of the mixedwater type near Manaus represent an ecotone (ADIS 1992); *Pachychernes baileyi* (Chernetidae), *Tyrannochthonius amazonicus* (Chthoniidae), *Geogarypus amazonicus* (Geogarypidae) and *Pachyolpium irmgardae* (Olpiidae) and *Dolichowithius minutus* (Withiidae) inhabit blackwater inundation forests in the valley of the Negro River. *Parachernes adisi* (Chernetidae) was collected from whitewater inundation forests along the lower Solimões River. *Paratemnoides minor* (Atemnidae) occurs in black- and whitewater inundation forests. *Pseudochthonius homodentatus* (Chthoniidae) lives in primary and secondary (non-flooded) upland forests of Central Amazonia.

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